Metapopulation Dynamics on Ephemeral Patches

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Abstract. A challenge for conservation management is to understand how population and habitat dynamics interact to affect species persistence. In real landscapes, timing and duration of disturbances can vary, and species' responses to habitat changes will depend on how timing of dispersal and reproduction events relate to the landscape temporal structure. For instance, increasing disturbance frequency may promote extinction of species that are unable to appropriately time their reproduction in an ever-changing habitat and favor species that are able to track habitat changes. We developed a mathematical model to compare the effects of pulsed dispersal, initiated by shifts in habitat quality, with temporally continuous dispersal. We tested the impacts of habitat (and population) turnover rates on metapopulation establishment, persistence, and long-term patch occupancy. Pulsed dispersal reduced patch occupancy and metapopulation longevity when habitat patches are relatively permanent. In such cases, demographic extinction was the primary form of local extinction. Conversely, when habitat patches are short-lived and new ones are frequently formed, pulsed dispersal promoted rapid colonization, increased occupancy and prolonged metapopulation persistence. Our results show that species responsiveness to habitat disturbance is critical to metapopulation persistence, having profound implications for the species likely to persist in landscapes with altered disturbance regimes.

Introduction

A challenge in metapopulation ecology and conservation management is to understand species persistence in anthropogenically and naturally disturbed landscapes. Early studies focusing on species occurrence at a landscape scale were underpinned by metapopulation ideas describing the dynamics of patch occupancy as a result of colonization and extinction of permanent habitat patches in a fixed landscape (Levins 1969; Hanski 1999). However, recent studies have modified the assumption of a static landscape (in terms of quality and suitability of patches) inserting more realism to metapopulation studies, for example assuming that species live in a dynamic landscape in which the habitat patches and the surrounding matrix are exposed to environmental stochasticity, habitat loss, succession or climate change (Stelter et al. 1997; Keymer et al. 2000; Amarasekare and Possingham 2001; Driscoll et al. 2013). A fully dynamic landscape could include changes in the availability, quality and position of both usable habitat (of various types) and nonhabitat areas ("matrix") that influence dispersal. In analogy to most metapopulation studies we consider models in which the habitat areas are dynamic but the nonhabitat areas are fixed in their effect on dispersal (see Blaum et al. 2012 for a discussion of the effects of a dynamic matrix).

In a dynamic landscape, the period for which patches remain unsuitable for species colonization and the frequency at which new suitable patches appear have strong effects on persistence of populations. High sensitivity to habitat disturbance due to life-history, such as altering propagule production rate and extinction proneness, makes the ability to follow landscape changes through time more dependent on species' dispersal ability (Thomas 1994; Keymer et al. 2000; DeWood et al. 2005). For instance, fast habitat turnover can reduce the rates at with individuals are spread across the landscape if individuals are not able to propagate in ephemeral habitats. Conversely, fast habitat turnover can benefit populations in which propagule production and release occur faster than habitat changes. Consequently, changes in disturbance regimes can alter community structure.

The study of the temporal structure of landscapes and disturbance regimes has important applications for habitat management. Restoration and/or the improvement of the quality of habitat patches and surrounding matrix can frequently alter disturbance and successional rates in landscapes, and may have both direct and indirect impact on species' dispersal rates, persistence and

distribution (Blaum et al. 2012; Driscoll et al. 2013). For example, fire suppression and flood control are commonly practiced, but it is generally unknown if and how the management of habitat dynamics may affect dispersal and subsequent metapopulation dynamics of organisms which are intrinsically linked to disturbances (e.g., through temporally pulsed dispersal).

Different dispersal strategies exist in relation to habitat condition and dynamics. Dispersal can be triggered by environmental disturbances or may even be intrinsically linked to habitat patch destruction, resulting in "pulsed dispersal". Thereby, disturbance or destruction of the habitat is not necessarily detrimental for the organisms, since they time the production of their dispersal stage with the onset of the disturbance (Bates et al. 2006; Altermatt and Ebert 2008), and emigration is trigged by the occurrence of the disturbance (Altermatt and Ebert 2010). Typical examples of organisms with pulsed dispersal are aquatic invertebrates, such as cladocerans, copepods, rotifers or ostracods, which survive desiccation of ponds in a drought-tolerant resting and dispersal stage (Altermatt and Ebert 2008).

Dispersal may also occur immediately prior to habitat patch destruction. For instance, dispersal in many organisms is strongly influenced by behavior (Crone et al. 2001; Fellous and Kaltz 2012; Bilton et al. 2001; Kubisch et al. 2013). In such situations, sensing changes in the environment by a few individuals can reinforce behavioral changes in others (Crone et al. 2001). Changes in dispersal behavior and dispersal-related morphology are known from organisms in which dispersal is triggered by population density, availability of resources or isolation of the habitat and often exhibits trade-offs with other life-history traits (Ahlroth et al. 2009; De Bie et al. 2012; Hanski et al. 2006).

For many organisms, the propensity to disperse or to produce dispersal stages is correlated with the type of habitat they live in (Southwood 1962). Although some organisms can exhibit both forms of dispersal, the numerically dominant form of dispersal within each generation (fractions of pulsed *vs* continuous dispersal) will have strong influence on the species persistence at dynamic landscapes. Species that are associated with temporary or rapidly changing habitats have generally higher levels (i.e., high fractions) of pulsed dispersal than species associated with permanent habitats (Southwood 1962). Empirical examples of such systems are agricultural landscapes in which habitable areas are

frequently changed by mowing and harvesting, lands in which flood and inundation events are frequent, or early successional communities in disturbed sites, where the habitat quality declines due to resource depletion and the timing for habitat to become suitable for re-colonization depends on disturbance (Stelter et al. 1997; Amarasekare and Possingham 2001; Blaum et al. 2012). In all of these systems dispersal is closely linked to the state of the habitat patch, and long-term survival in such habitat systems depends on the timing of dispersal. Since long-term survival depends on an adequate dispersal strategy, strong selection on dispersal timing may be expected.

Species may be classified according to their dispersal behaviors and the longevity of habitat patches (table 1), which can affect the longevity of populations. Populations may be either short-lived (one or a few generations) or long-lived, surviving for numerous generations. If habitat turnover is low and patches are long-lived, we would expect demographic extinction to be the most frequent cause of extinction, whereas habitat patch turnover may create extinction itself as the rate of patch destruction increases. Although many of the examples studied in table 1 have focused on metapopulation occupancy and viability in a dynamical landscape, no link between different dispersal forms and the frequency in which disturbance occurs at landscape has been investigated. We therefore asked a series of interrelated questions about how metapopulation persistence and dynamics are affected by habitat patch dynamics and the timing of dispersal events relative to habitat patch destruction. First, how do different dispersal behaviors affect the probability of population establishment at different degrees of habitat patch turnover? Second, once established, how do species' dispersal behaviors influence patch occupancy through time in a dynamic landscape? Finally, how do changes in population-habitat turnover rates affect dispersal occurrence, probability of metapopulation establishment and persistence? We used a continuous-time, stochastic patch-occupancy model with habitat dynamics to address these questions. We draw general conclusions about how habitat management and modification of disturbance regimes facilitates or impedes metapopulation persistence.

Model and Methods

The stochastic and mean-field models. We analyzed metapopulation dynamics in landscapes composed of a finite number of ephemeral patches (N) that are either suitable or unsuitable for colonization by a given species. Consequently, patches in a landscape are in one of three possible states, $S \in \{0, 1, 2\}$: unsuitable and unoccupied ($S = 0$), suitable and unoccupied ($S = 1$), suitable and occupied ($S = 2$). The dynamics of habitat suitability are determined by three parameters, λ, β_1 and β_2 (fig.1). Unsuitable patches become suitable at a rate λ. Suitable patches may become unsuitable due to a mixture of external and internal drivers. Hence, unoccupied, suitable patches and occupied suitable patches may become unsuitable at different rates (β_1 and β_2, respectively). When $\beta_1 = \beta_2$, the dynamics of habitat suitability are independent of patch occupancy. If $\beta_2 > \beta_1$, then occupancy decreases the lifetime of a suitable patch.

Populations residing in a suitable patch produce propagules continuously at rate c_1 and a pulse of c_2 propagules when their patch becomes unsuitable (fig.1). The net colonization rate is

$$c = c_1 + c_2\beta_2. \tag{1}$$

Populations in an occupied patch go extinct either because their patch becomes unsuitable or at a rate e due to other sources of local extinction, including disturbances unrelated to the habitat dynamics and demographic extinction.

The stochastic model is given by a continuous-time Markov chain process whose state is characterized by the total number N_0 of unsuitable patches, the total number N_1 of suitable but unoccupied patches, and the total number N_2 of occupied patches. Since all patches must be in one of these three states, $N_0 + N_1 + N_2 = N$. The model exhibits two types of changes in patch state. First, there are changes of state due to empty patches becoming suitable or unsuitable, occupied patches becoming suitable, local demographic extinction, or colonization from an occupied patch which occur at rates λ, β_1, β_2, e, and $c_1 N_2/N$ (fig. 1). We interpret these rates roughly as follows: over a short time interval of length Δt, the probability at which an unsuitable patch becomes suitable is approximately $\lambda\Delta t$, the probabilities that occupied or unoccupied patches become unsuitable are

approximately $\beta_1 \Delta t$ and approximately $\beta_2 \Delta t$, respectively, and the probability that an occupied suitable patch leads to colonization of an empty, suitable patch is approximately $(c_1 N_1/N)\Delta t$. The second type of changes in patch state occurs when an occupied patch becomes unsuitable. Dispersal results in individuals leaving the patch simultaneously and subsequently colonizing empty patches. During a pulsed dispersal event, each suitable and unoccupied patch is colonized with probability c_2/N. When N is large, pulsed dispersal events lead to approximately a Poisson distributed number of colonization events with mean $p_1 c_2$.

When the number of patches N is sufficiently large, the dynamics of the stochastic model are well approximated by a mean-field model (Kurtz 1978). For this mean-field model, let $p_i = N_i/N$ denote the fraction of patches in state $i = 0, 1, 2$. The dynamics of the mean field model are given by the following system of differential equations:

$$\begin{aligned} \frac{dp_0}{dt} &= \beta_1 p_0 + \beta_2 p_2 - \lambda p_0 \\ \frac{dp_1}{dt} &= \lambda p_0 - c p_1 p_2 - \beta_1 p_1 + e p_2 \\ \frac{dp_2}{dt} &= c p_1 p_2 - (e + \beta_2) p_2. \end{aligned} \tag{2}$$

Numerical and analytic approaches. We studied the mean-field and stochastic models using a mixture of analytic and numerical approaches. For the mean field model, we examined metapopulation persistence and equilibrium occupancies using standard techniques from dynamical systems. This analysis is presented in Appendix A. Numerical solutions for the mean field model were computed with the DeSolve package of R (R Development Core Team 2012).

To estimate the probability of establishment of a metapopulation for the stochastic model we used a branching process approximation of the Markov chain when the number of patches is sufficiently large. The approximation assumes that there are sufficiently many patches that the fluctuations in p_1 around the unoccupied landscape equilibrium $p_1^* = \frac{\lambda}{\lambda + \beta_1}$ are sufficiently small that they can be ignored. This assumption is supported by numerical simulations of the full stochastic model. We show in Appendix B that the establishment probability $1 - s$ can be approximated by the smallest

positive fixed point of the following for the branching process:

$$g(s) = \frac{1}{1 + \frac{c_1}{e+\beta_2} p_1^*(1-s)} \left(\frac{e}{e+\beta_2} + \frac{\beta_2}{e+\beta_2} \exp(c_2 p_1^*(s-1)) \right).$$

To solve for this fixed point numerically, we used the standard method of computing $g^t(0)$ for sufficiently large t (Harris 2002).

Unlike the mean field models, pulsed and continuous dispersal events differently impact the stochastic dynamics for a fixed colonization rate c. Consequently, for our analysis of the stochastic models, we introduce a parameter, α, corresponding to the fraction of colonization events, on average, due to pulsed dispersal. The extreme of $\alpha = 0$ represents species that only disperse continually during the habitat lifetime, and when a patch is destroyed, the population goes extinct. Alternatively, $\alpha = 1$ represents species that disperse only when disturbances occur. While some species exhibit a dominant form of dispersal (i.e. $\alpha = 0$ or 1), some species can display both modes of dispersal. With this notation, the quantities $c_2\beta_2 = \alpha c$ and $c_1 = (1-\alpha)c$ describe the relative contributions of pulsed and continuous dispersal events.

The effects of dispersal behavior and landscape dynamics on stochastic fluctuations and metapopulation viability are analyzed using numerical simulations with Gillespie's algorithm (Gillespie 1977) in R. We examined three habitat-population turnover rates in which population lifespan ($1/e$) is longer, similar and shorter than the habitat lifetime ($1/\beta_2$). The measures for habitat-population turnover rates were based on empirical examples found in nature (table 1). For each parameter combination we ran 100 simulations for 5000 time units. For larger landscapes ($N = 1600$ patches), the metapopulations always persisted for the entire duration of the simulation and we analyzed the temporal changes in the number of suitable empty and suitable occupied patches using cross-correlation analyses. We concluded our analyses by examining the persistence time of smaller landscapes ($50 < N < 1500$ patches) to identify minimal landscape size (i.e., minimal number of patches) for metapopulation viability.

Results

Long-term metapopulation persistence and patch occupancy. Long-term metapopulation persistence for the mean field model is determined by the reproductive number R_0 of an occupied patch in a largely empty landscape. This reproductive number corresponds to the number of patches colonized by an occupied patch during its "lifetime" in a mostly unoccupied landscape. When this reproductive number is greater than one, a population in an occupied patch colonizes more than one patch before going locally extinct. Hence, the number of occupied patches tends to increase provided $R_0 > 1$. Conversely, when $R_0 < 1$, occupied patches do not replace themselves on average and the metapopulation tends to go deterministically toward extinction. Landscape and population characteristics simultaneously determine the reproductive number R_0. Specifically, colonization and extinction rates regulate the propagule production by local populations and the lifespan of occupied patches. Habitat dynamics determine the availability of suitable habitat and trigger dispersal events. Taking into account these factors, R_0 is the product of three terms: the mean lifetime of an occupied habitat patch, τ, the equilibrium fraction of suitable patches when the landscape is unoccupied, s and the species colonization rate, $c_1 + c_2\beta_2$.

The mean lifetime of an occupied habitat patch τ, represents the time before it becomes unoccupied either due to demographic extinction or a shift in habitat suitability:

$$\tau = \frac{1}{e + \beta_2} \tag{3}$$

The second component s, corresponds to the equilibrium fraction of suitable habitat when the landscape is unoccupied:

$$s = \frac{\lambda}{\lambda + \beta_1} \tag{4}$$

Intuitively, when disturbance rates are faster than the creation of new habitat patch rates (i.e., $\beta_1 > \lambda$) the amount of suitable habitat, s, is small and restricts colonization success. The mean number of propagules produced by an occupied patch is given by $\tau(c_1 + c_2\beta_2)$. The reproductive

number of the metapopulation is the product of τ, s, and $c_1 + c_2\beta_2$:

$$R_0 = s\tau c = \frac{\lambda}{\lambda + \beta_1}\frac{c_1 + c_2\beta_2}{\beta_2 + e} \tag{5}$$

When $R_0 > 1$, the metapopulation persists at a globally stable, positive equilibrium (see Appendix A) given by:

$$\begin{aligned} p_0^* &= 1 - p_1^* - p_2^* \\ p_1^* &= \frac{\beta_2 + e}{c_1 + c_2\beta_2} \\ p_2^* &= 1 - \frac{\beta_2}{\lambda + \beta_2} - \frac{(\lambda + \beta_1)(e + \beta_2)}{(c_1 + c_2\beta_2)(\lambda + \beta_2)}. \end{aligned} \tag{6}$$

When $R_0 < 1$, the metapopulation goes to extinction for all initial conditions (see Appendix A). Equations (5) and (6) imply that the reproductive number and the equilibrium patch occupancy (p_2^*) increase with colonization rates c_1 and c_2, decrease with local extinction rate e, and increase with the rate λ at which unsuitable habitat becomes suitable.

Changes in patch states may occur when patch suitability depends on the availability of a depleted resource (i.e., $\beta_1 = 0$ but $\beta_2 > 0$). In this kind of dynamical landscape scenario, $1/\beta_2$ is the mean time the population draws down the resource and $1/\lambda$ is the mean recovery time for the resource. For this landscape scenario, the effect of β_2 on metapopulation persistence and equilibrium occupancy depends on the mean number of colonizers (c_1/e) produced by a patch prior to demographic extinction and the mean number of colonizers (c_2) produced by a pulsed dispersal event. When pulsed dispersal produces more colonizers than continuous dispersal (i.e., $c_2 > c_1/e$), increasing the rate at which habitat becomes unsuitable increases the metapopulations reproductive number (fig. 2A). Intuitively, the loss of colonizers prior to the pulsed dispersal event is over-compensated for by the increased frequency of pulsed dispersal events. Consistent with the effect of β_2 on R_0, increasing β_2 increases the equilibrium patch occupancy at low values of β_2 (fig. 2B). However at high levels of β_2, increasing β_2 reduces the persistence time of occupied patches enough to cause

a reduction in equilibrium patch occupancy. On the other hand, when continuous dispersal produces more colonizers than pulsed dispersal ($c_1/e > c_2$), increasing β_2 decreases both R_0 and the equilibrium patch frequency.

An alternate habitat dynamic occurs when changes in habitat suitability are driven purely by exogenous factors and all suitable patches, unoccupied or occupied, experience the same habitat shift rate. For this landscape scenario, the effect of $\beta = \beta_1 = \beta_2$ on the metapopulation reproductive number and equilibrium patch occupancy depends in a subtle manner on the mean number of colonizers produced during a dispersal event (c_2), the mean number of colonizers produced prior to a demographic extinction event (c_1/e), and the mean number of colonizers lost during the time a patch remains unsuitable (c_1/λ). When $c_2 > c_1/e + c_1/\lambda$, this causes R_0 and p_2^* to exhibit a humped-shaped relationship with β (fig. 2C, D); increasing at low β and decreasing at high β. Under these circumstances, the metapopulation only persists at intermediate rates of suitable patches becoming unsuitable. On the other hand, when $c_2 < c_1/\lambda + c_1/e$, increasing rates at which patches become unsuitable always decreases R_0 and p_2^*, and there is a critical β value above which metapopulation persistence is no longer possible.

Establishment, stochastic fluctuations, and persistence in finite landscapes. While the mean-field model provides useful insights into persistence and long-term patch occupancy for landscapes with a large number of patches, stochastic effects play a significant role in metapopulations with fewer patches. Stochastic effects also generate fluctuations of varying magnitudes around the mean field equilibrium, and ultimately determine metapopulation viability in landscapes with a finite number of patches (see online supplementary fig. A1). Using the stochastic model, we analyzed how different dispersal behaviors influence establishment, the covariance structure of fluctuations between suitable unoccupied and occupied patches on the event of establishment (i.e., spatio-temporal variance in patch occupancy), and persistence times for established metapopulation.

Metapopulation establishment probability. Using the analytical approximation described in the methods section, our analysis (see Appendix B) reveals that the effect of pulsed dispersal on metapopulation establishment depends on the relative lengths of population lifespan ($1/e$) and habitat lifespan ($1/\beta_2$). When the habitat lifespan is long relative to the population lifespan (cases 3 and 4, table

1), pulsed dispersal has a positive effect on metapopulation establishment; metapopulations with a higher propensity for pulsed dispersal are more likely to establish (gray dotted curves in fig.3). In contrast, when the habitat lifespan is short relative to the population lifespan (cases 5 and 6, table 1), metapopulations with a higher propensity for pulsed dispersal are less likely to establish (black dashed curves in fig.3). These differences do not stem from differences in the mean colonization rates as they are unaffected by the fraction of the population exhibiting pulsed dispersal. Instead these differences stem from the variation in the number of patches colonized by an occupied patch during its lifetime; greater variation in the number of patches colonized results in lower establishment probabilities, as we now explain. When the population lifespan is short relative to the habitat lifespan (cases 3 and 4, table 1), pulsed dispersal leads to greater variation in the number of patches colonized (see Appendix B). Intuitively, the reproductive number of a patch R_0, in this case, is achieved by most occupied patches going extinct prior to colonizing other patches, while a few occupied produce large, pulsed colonization events. Consequently, when habitat lifespan is long, pulsed dispersal creates greater variation in propagules produced and thereby decreases the likelihood of establishment. Conversely, when the habitat lifespan is short relative to the population life span, most occupied patches produce a somewhat similar number of pulsed dispersers. Subsequently, pulsed dispersal produces less variation in the number of colonized patches and increases the likelihood of establishment.

Fluctuations in patch occupancy. When a metapopulation has established in a landscape, it can persist for a long time and exhibit meta-stable behavior. During this period, patch occupancies tends to fluctuate around the equilibrium p_0^*, p_1^*, p_2^* of the mean-field model. Using numerical simulations, we examined how population lifetimes and habitat lifetimes in conjunction with dispersal mode influence the spatial and temporal covariance structure of these fluctuations. More specifically, we considered three landscape scenarios (see online supplementary fig.A2) in which population lifetimes are longer (cases 5 and 6, table 1), shorter (cases 3 and 4, table 1), and similar (cases 1, 2, 7 and 8, table1) to habitat lifetimes, that is, $1/e \gg 1/\beta_2$, $1/e \approx 1/\beta_2$, and $1/e \ll 1/\beta_2$, respectively. When population lifetimes are longer than habitat lifetimes, patch destruction is the main factor reducing patch occupancy. On the other hand, when population lifetime is short relative to habitat lifetime,

demographic extinction of local populations is the main factor reducing patch occupancy (online supplementary fig. A2).

When population lifetime is short relative to habitat lifetime, the variance in patch occupancy increases with the frequency of pulsed dispersal (black dashed line in fig. 4A). As in the case of metapopulation establishment, the mean colonization rate for pulsed dispersers is achieved by rare, yet pronounced, pulsed dispersal events. Thereby, pulsed dispersal increases the temporal variance in patch occupancy, and changes in suitable occupied patches and unoccupied patches are tightly coupled and negatively correlated; reductions in occupied patches typically correspond to increases in unoccupied, suitable patches (black dashed line in fig. 4B).

When average population lifetime is longer than habitat lifetime, pulsed dispersal occurs more frequently and is balanced by higher colonization rates, which buffers the effects of patch disturbance. Under these circumstances, pulsed dispersal decreases the variation in patch occupancy (gray dotted line in fig. 4A). Although negatively correlated, changes in occupied and unoccupied patch states becomes less coupled since loss of a patch is followed by high production of colonizers, making changes in number of occupied patches higher than changes in unoccupied ones (gray dotted line in fig. 4B). This decoupling reduces variation in patch occupancy.

Metapopulation viability. To address how dispersal mode influences metapopulation viability, we considered an established metapopulation starting at patch occupancy equilibrium p_0^*, p_1^*, p_2^* of the mean-field model and computed the mean of persistence time across 100 replicates. This was done for a range of landscape sizes. Figure 5A shows how the frequency of pulsed dispersal and landscape size influence persistence in landscapes with short population lifetimes relative to habitat lifetimes (high e/β_2 ratio, cases 3 and 4, table 1). Intuitively, mean persistence time increases with landscape size. When pulsed dispersal is an uncommon dispersal mode, mean persistence time increases and saturates rapidly with landscape size, and the critical landscape size is approximately 200 patches. However, when pulsed dispersal is the most common dispersal mode, mean persistence time increases gradually with landscape size even at large patch numbers. Intuitively, pulsed dispersal in environments where populations are highly prone to extinctions results in greater fluctuations in the metapopulation dynamics and, consequently, in shorter persistence times.

To examine the effect of landscape size, habitat turnover and dispersal mode on metapopulation viability, we defined the minimum viable metapopulation (MVM) size to be the minimum number of patches resulting in a 90% chance of a metapopulation persisting at least $5,000$ time steps. When habitat lifespan is greater than expected population lifespan (cases 3 and 4, table 1), pulsed dispersal allows high persistence at small landscape sizes (gray dotted curve in fig. 5B). Alternatively, for short-lived populations (high e/β_2 ratios), metapopulations displaying a high fraction of pulsed dispersal only persist in larger landscape sizes (black dashed curve in fig. 5B).

Discussion

The majority of metapopulation studies predict that ephemeral or small habitat patches have a negative effect on metapopulation persistence (Lande 1987; Tilman et al. 1994; Gyllenberg and Hanski 1997; Bascompte and Solé 1998; Hill and Caswell 1999). These predictions, however, are largely based on the assumption that disturbances and dispersal/colonization dynamics are uncorrelated (Keymer et al. 2000; Amarasekare and Possingham 2001; DeWoody 2005; Xu et al. 2006). Modeling habitat disturbance and species' dynamical processes separately is a straightforward way to understand extinction processes (in terms of species' life history) and patch destruction factors (Fahrig 1992; Keymer et al. 2000; Amarasekare and Possingham 2001; DeWoody et al. 2005). However, in many systems the effects of patch disturbance and the timing of dispersal are not independent (Bowler and Benton 2005; see also table 1). Species inhabiting naturally disturbed habitats often disperse in response to changes in habitat quality in a manner that enhances their survival in these environments (Dennis et al. 2003; Bowler and Benton 2004).

Although the existence of pulsed dispersal has been documented in empirical studies (Crone et al. 2001; Bates et al. 2006; Altermatt and Ebert 2010; see also table 1), theoretical work has focused only on dispersers originating from patches before the actual occurrence of disturbances. Such dispersal has been modeled commonly in a continuous way, neglecting the "pulsed release" of dispersers when a patch is destroyed. Here, we analyzed mean-field and stochastic models to study how continuous and pulsed dispersal affects metapopulation persistence and patch occupancy at different habitat and population turnover rates. Our chosen set of model parameters and especially

the suite of chosen habitat and patch turnover rates reflect a large and realistic range of natural systems (see table 1 for examples). We also checked the impact of population-habitat turnover rates on metapopulation viability, motivated by different examples of dispersal behavior and population lifespan related to the habitat species live in.

Metapopulation establishment and persistence in highly-disturbed landscapes. A necessary condition for metapopulation establishment and long-term persistence is that the reproductive number of populations is greater than one. It can be interpreted as the "infective" characteristic of a particular metapopulation to expand its range across the landscape and can be used as a criterion to define the invasion potential for populations given their colonization-extinction dynamic and the landscape's temporal structure (Keymer et al. 2000). Previous theoretical studies have used R_0 to define a threshold for particular habitat loss and restoration turnover rates in which metapopulation persistence becomes impossible (Keymer et al. 2000; DeWoody et al. 2005; Xu et al. 2006). In these models, the impact of habitat loss due to disturbances is directly related to reduction of number of local populations that contribute propagules to maintain colonization rates that are higher than extinction rates. However, these models have neglected the effects of pulsed dispersal on R_0.

The occurrence of pulsed dispersal helps to maintain R_0 higher than one when the number of propagules released after disturbance is capable of maintaining a high number of occupied patches, even at high disturbance rates. However, our results show that the metapopulation occupancy is dependent not only on R_0, but also on the recovery rates of habitats, which need to be high enough to provide a minimal number of patches for metapopulation viability. For cases in which occupancy of patches leads to occupied patches becoming unsuitable, depletion rates of patches produce higher reproductive numbers and patch occupancy (fig. 2A, B). High turnover of patches favors species that have pulsed dispersal as a dominant form of dispersal. Conversely, when suitable occupied and suitable empty patches are equally subject to habitat change, the amount of propagule releases by pulsed dispersal over-compensates for the low colonization rates prior to habitat destruction (fig. 2C, D). However, in this case, the increasing destruction of patches should be followed by high restoration rates of patches to maintain R_0 higher than one and a minimal metapopulation occupancy. If the

rates of patch restoration are slower than habitat destruction rates, the metapopulation can easily go extinct. These results call for attention in the context of defining the "optimal disturbance frequency" at the landscape level, which varies according to the kind of patch disturbance in which landscape are exposed and can have different consequences for persistence of species, specially when they release different propagule fractions during and after patch disturbance.

The interplay between population reproductive number and dispersal behavior is essential to understand colonization rates and patch occupancy during invasion processes in landscapes composed of ephemeral patches (McArthur and Wilson 1967; Kot and Lewis 1996). Studies have shown that successful invasion is positively correlated with high dispersal frequency and a large amount of individuals sent during dispersal events (Jules et al. 2002; Schreiber and Lloyd-Smith 2009). Extending these results to our dynamical landscape context, we found that when dispersal is linked to disturbance frequency, high levels of habitat turnover lead to more propagules released, increasing the probability of establishment success of invasive species in the new landscape. In this form, the increase of disturbance frequencies can promote a successful introduction and spread of invasive species across landscapes, especially when invasive species are capable of exhibiting pulsed dispersal and the frequency of patch turnover is high.

For already established metapopulation systems, the key factor determining species persistence in dynamic landscapes is their capability to maintain per-patch colonization rates greater than disturbance rates (Keymer et al. 2000; Hastings 2003). Populations that display only temporally continuous dispersal are less tolerant to high frequency disturbance regimes, since increased disturbances negatively affects the population lifespan and make extinction rates higher than colonization rates. Conversely, when the predominant form of population dispersal is pulsed, it creates a positive link between dispersal and disturbance, in that colonization rates become higher when rates of habitat loss are higher, ensuring a minimum level of patch occupancy for metapopulation persistence. Therefore, ephemeral landscapes are not always detrimental for metapopulations.

Short-lived populations inhabiting dynamical landscapes. We demonstrated the importance of positive links between dispersal and disturbance for population persistence when the lifetime of habitat is shorter than population lifespan. However, for some biological systems, population lifespan can

be shorter than habitat lifetime. For example, human interventions or natural environmental factors can affect successional and other processes, such that the generation of new habitats is reduced. Hence, species specialized in tracking successional habitat can be driven to extinction in managed landscapes, where the creation of new habitat is practically zero (Thomas 1994; Stelter et al. 1997). For species living in ephemeral habitats and in which dispersal is tightly linked to the disturbance of habitat (pulsed dispersal dominates), the colonization of new patches becomes difficult and species may eventually go extinct at the metapopulation level when population turnover is faster than habitat turnover.

Our results show that when patch disturbance is the main factor promoting changes in patch occupancy, the metapopulation dynamic becomes close to a source-sink dynamic and high occupancy is achieved when colonization events are promoted by the occurrence of habitat disturbances. Conversely, at high disturbance frequencies, occupied patches act as sources of new dispersers and high propagule release during disturbance is important to increase patch occupancy and the probability of persistence. This is also distinct from the case where the main factor causing reduction in patch occupancy is demographic extinction, in which case the dispersal and colonization rates are supported by the amount of populations surviving disturbances. Then, the metapopulation dynamic becomes close to classic metapopulation dynamics and the continuous propagule release during patch occupancy balances the negative effects of population extinctions.

Shifts between patch disturbance and demographic extinction domains can happen in natural landscapes due to many external drivers already mentioned, which are then interchanging the metapopulation organization of the system. Such shifting effects on metapopulation organization have already been documented in previous studies (Stelter et al. 1997; Hastings 2003). In agreement with these studies, our findings show that changes in timing of disturbance occurrences related to population lifespan deeply affected the criterion for minimum per-patch colonization rates that are sufficient to maintain a metapopulation. The negative impacts coming from the shift between disturbance domain to demographic extinction domain governing patch occupancy are likely to be more drastic for populations with dispersal linked to habitat changes. For these cases, the advantages of high fractions of pulsed dispersal on population colonization rates are restricted to

metapopulations living in landscapes composed by high number of habitat patches, when pulsed dispersal ensures colonization rates higher than extinction rates (fig. 5). In small landscapes we found high fluctuations and consequently low patch occupancy and high extinction risks.

Implications for conservation and management of species. Landscapes composed of ephemeral patches are not only diverse and contain specialized communities, but also depend on a proper adoption of management strategies which balance the positive and negative effects of patch destruction, creation and suppression of disturbances (Stelter et al. 1997; Keymer et al. 2000; Hastings 2003). The modification of habitat-patches and the surrounding areas can extensively change the landscape and make the habitat and matrix more or less hostile for species. For successful land-management practices, it is necessary to understand critical processes influencing species presence in dynamical landscapes. Here, we for the first time specifically addressed the role of dispersal behavior relative to disturbance, and how it shapes the relationship between populations and their habitat in situations when patch and population turnover are coupled or not.

In table 1 we show how metapopulation systems can differ in respect to population/habitat longevity rates and dispersal modes. The management of systems in which demographic extinction rates are similar (cases 1-2, 7-8, table 1) or higher than habitat patches turnover rates (cases 3-4, table 1) vary in the conservation plan required to ensure persistence, depending on species' dispersal behavior. For species exhibiting continuous dispersal during the habitat lifetime, efforts to improve habitat quality can promote dispersal and positive impacts on metapopulation dynamics. However, if the focal species has a predominantly pulsed dispersal behavior, it is necessary to invest in increasing the amount of habitat to maintain the species at the landscape level.

For cases in which habitat turnover is faster than demographic extinction (cases 5-6, table 1), frequent habitat manipulation/restoration can increase the persistence probability for species that are capable of pulsed dispersal. For example, for landscapes mosaics formed by short-term crop systems, the manipulation of spatio-temporal distribution of host plants can be a useful strategy to control and reduce the incidence of pest insects that disperse in pulses after harvest. When these species are capable of using alternative host plants as refuge during the absence of the primary host plant, creating gaps in time between the succession of crops can restrict the spread and consequently

the economic damage caused by these species (Fitt et al. 2005; Tilman et al. 2009). The different practices for management of burnt wood after fire occurrence is another example of how habitat disturbs and dispersal can affect occupancy of species. The management of burned forest areas also affect the recovery rate by affecting the number of seed predators which destroy the dispersal propagules. Studies have shown that post-fire polices of removal of burnt trunks and remaining debris from burnt areas can increase the vegetation restoration rates by reducing the predation of seed from these areas (Puerta-Piñero et al. 2010).

Our theoretical study calls attention to the importance of shift between organizational systems of metapopulation dynamics for species with different dispersal behavior. Since in real landscapes the time and duration of disturbances can be quite variable, populations can face temporal changes between dynamical regimes or live in spatial-temporal mosaics, with mixtures of the two dynamical regimes. Different dispersal behavior may or may not facilitate species persistence, depending on landscape features such as size and disturbance regime. Our general results can be used for a wide range of species (table 1) and help to estimate how anthropogenic and natural changes of the temporal structure of landscapes can influence metapopulation viability.

Acknowledgments

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Appendix

Appendix A - Analysis of Mean Field Model. Using the fact that $p_0 + p_1 + p_2 = 1$, we can rewrite (5) as a planar system:

$$\begin{aligned} \frac{dp_1}{dt} &= \lambda(1 - p_1 - p_2) - cp_1p_2 - \beta_1 p_1 + ep_2 =: f(p_1, p_2) \\ \frac{dp_2}{dt} &= cp_1p_2 - (e + \beta_2)p_2 =: g(p_1, p_2). \end{aligned} \tag{7}$$

The line $p_2 = 0$ is invariant and restricted to this line, the system is linear with a globally stable equilibrium $p_1 = s := \frac{\lambda}{\lambda+\beta_1}$. The "per-patch" growth rate of occupied patches at the equilibrium $(s, 0)$ is given by $cs-(e+\beta_2)$. Hence, the equilibrium $(s, 0)$ is locally unstable when $R_0 := \frac{cs}{e+\beta_2} > 1$ and locally stable when $R_0 < 1$. When $R_0 > 1$, there is a positive equilibrium given by (p_1^*, p_2^*) as defined in the main text. Linearizing about this equilibrium and using the trace-determinant criterion reveals that this equilibrium is locally stable whenever $R_0 > 1$.

To verify that local stability implies global stability for this system, we use the Dulac function $\phi(p_1, p_2) = \frac{1}{p_2}$ which is strictly positive and well-defined for $p_2 > 0$. Since

$$\frac{\partial}{\partial p_1} f(p_1, p_2)\phi(p_1, p_2) + \frac{\partial}{\partial p_2} g(p_1, p_2)\phi(p_1, p_2) = -\frac{\lambda + \beta_1}{p_2} - c < 0$$

for $p_2 > 0$, it follows from the Dulac criterion that this planar system has no periodic orbits or heteroclinic cycles in the positive orthant. Applying the Poincaré-Bendixson Theorem implies that $(s, 0)$ is globally stable whenever $R_0 < 1$ and (p_1^*, p_2^*) is globally stable (in the positive simplex) whenever $R_0 > 1$.

Appendix B - Establishment probability. When N is large, we can approximate the establishment dynamics of the number N_2 of occupied patches with a continuous time branching process for which there are three types of events: (1) an occupied patch goes extinct, $N_2 \mapsto N_2 - 1$, at rate $(e + \beta_2)N_2$, (2) an unoccupied suitable patch becomes occupied, $N_2 \mapsto N_2 + 1$, at rate $c_1 N_2$, or (3) a pulsed dispersal event, $N_2 \mapsto N_2 - 1 + Z$ where Z is poisson with mean c_2, at rate $\beta_2 N_2$.

Then, the number of patches colonized by an unoccupied patch during its life time is given by the sum of two random variables $X+Y$. Corresponding to the contribution due to continuous dispersal, X is a geometric random variable with mean $R_1 = \frac{c_1 s}{e+\beta_s}$. Corresponding to the contribution due to pulsed dispersal, $Y = Y_1 Y_2$ where Y_1 is a bernoulli random variable with probability of success $\frac{\beta_2}{e+\beta_2}$ and Y_2 is a poisson random variable with mean $c_2 s$. The probability generating function of X is given by

$$g_1(s) = \frac{1}{1 + R_1(1 - s)}$$

and the probability generating function for Y is given by

$$g_2(s) = \frac{e}{e+\beta_2} + \frac{\beta_2}{e+\beta_2}\exp(c_2 s(s-1)).$$

Since X and Y are independent random variables, the probability generating function for $X+Y$ is

$$g(s) = g_1(s)g_2(s)$$

as claimed in the main text. The limit theorem of branching processes (see, e.g., Chapter 1 of Harris 2002) implies that the probability of extinction of this branching process (assuming initially one patch is occupied) is given by the smallest positive fixed point q of g. When $R_0 \leq 1$, $q = 1$ (i.e. extinction occurs with probability one). When $R_0 > 1$, $q \in (0,1)$ (i.e. there is a positive probability of establishment). As $g^t(0)$ equals the probability of being extinct by generation t (assuming initially one patch is occupied), $q = \lim_{t\to\infty} g^t(0)$ can be approximated by $g^t(0)$ for t sufficiently large.

Define $R_2 = \frac{\beta_2 c_2 s}{\beta_2 + e}$ to be the expected number of patches colonized due to pulsed dispersal. Notice that $R_0 = R_1 + R_2$. Suppose that $\beta_2 \gg e$ (i.e. population lifetime is long relative to habitat lifetime). Consider ways to achieve the same R_0: (1) $R_1 = R_0$, $R_2 = 0$ or (2) $R_1 = 0$, $R_2 = R_0$. These scenarios correspond to purely continuous dispersal and purely pulsed dispersal. Since $X+Y = Y$ is geometric in the first case and approximately Poisson in the second case, a standard calculation (see, e.g., Lloyd-Smith et al. 2005) shows that the probability of extinction is greater in the first case than in the second case. This difference stems from the fact that the geometric distribution has a larger variance (given the same mean) than the Poisson distribution.

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Table

Empirical examples of metapopulations that exhibit different levels of population turnover (e, demographic extinction) and habitat patch turnover (β_2, patch destruction). For all scenarios of e/β_2 ratios, we give examples where dispersal is mostly continuous or pulsed. The mode of dispersal refers to the numerically dominant form of dispersal within each generation at a spatial scale that is consistent with interpatch dispersal (and metapopulation dynamics). The different e/β_2 ratios reflect the scenarios explored in our mathematical models.

Cases	Population longevity (e, demographic extinction)	Habitat patch longevity (β_2, patch destruction)	e/β_2 ratio	Dispersal	Examples	References
Case 1	short (high e)	short (high β_2)	~ 1	continuous	Both populations and patches are prone to high extinctions and turn-over. Possible scenarios are subsets of island-patches in a mainland-island (or source-sink) system, where island populations and island habitat patches are in a constant turn-over. Examples: Copepods of the genus *Tigriopus* living in tidepools, where demographic extinctions and patch destruction (desiccation without drought tolerant resting stages) is common. Possibly, a source/mainland (as observed in the bay checkerspot *Euphydryas editha* mainland-island metapopulation) is needed to maintain overall persistence with both high e and β_2	Harrison et al. 1988; McLaughlin et al. 2002; Johnson 2001; Altermatt et al. 2012.
Case 2	short (high e)	short (high β_2)	~ 1	pulsed	Insects colonizing carrion or dung. Resource (carrion or dung) persists long enough for the development of one generation. Neotropical flower mites that inhabits inflorescences of palms and need to be transported to new flowers by other flower visitors (i.e. phoretic dispersal) towards the end of flower's life-time. In both cases are observed 100% pulsed dispersal at the end of resource (i.e patch) life-time.	Roslin 2001; Roslin and Koivunen 2001; Fronhofer et al. 2013.
Case 3	short (high e)	long (low β_2)	high	continuous	Organisms with small populations on persistent patches. The small populations are prone to fast population turnover due to drift or demographic processes, while dispersal is independent of population size and patch state. Examples: glanville fritillary (*Melitaea cinxia*), valley elderberry longhorn beetle (*Desmocerus californicus*), American pika (*Ochotona princeps*).	Collinge et al. 2001; Hanski et al. 1995; Hanski et al. 2006; Smith and Gilpin 1997; Talley 2007.
Case 4	short (high e)	long (low β_2)	high	pulsed	Organisms in which population dynamics or fluctuations in environmental conditions may forecast population extinctions and thereby trigger pulsed dispersal (e.g., through behavioral changes). Example: voles.	Crone et al. 2001.

Cases	Population longevity (e, demographic extinction)	Habitat patch longevity (β_2, patch destruction)	e/β_2 ratio	Dispersal	Examples	References
Case 5	long (low e)	short (high β_2)	low	continuous	Herbivorous insects with large population sizes (i.e., low risk of demographic extinctions) living on early successional plants (e.g., thistles). Continuous production of disperses is an insurance against plant (= habitat patch) loss. Examples: Canada thistle gall fly (*Urophora cardui*) or planthoppers (e.g., *Prokelisia crocea* and *Anagrus columbi*).	Cronin 2004; Eber and Brandl 2003.
Case 6	long (low e)	short (high β_2)	low	pulsed	Rock pool invertebrates with large populations that are not very prone to demographic extinctions. Desiccation of pools is common and pulses passive dispersal through drought tolerant resting stages. Examples: water fleas (*Daphnia* sp.), copepods, or ostracods.	Altermatt and Ebert 2008; Altermatt and Ebert 2010; Vanschoenwinkel et al. 2008.
Case 7	long(low e)	long (low β_2)	~ 1	continuous	Epiphytic plants (e.g., moss or lichens) on tree trunks. Relatively little turn-over in habitat patch (tree trunks are persisting for a long time), and few demographic extinctions. Generally, rather stable and predictable habitats and population dynamics. Continuous production of dispersers (spores in the case of moss). In a study on a metapopulation of the epiphytic moss *Neckera pennata*, demographic extinctions could be neglected, and turn-over was slow.	Snäll et al. 2005; Werth et al. 2006.
Case 8	long (low e)	long (low β_2)	~ 1	pulsed	Species in which both population and habitat turnover is long, but where the production of dispersal stage is only happening at irregular events, such as in masting years (e.g., oaks) or at rare climatological conditions (e.g., exceptionally long seasons in alpine plants).	

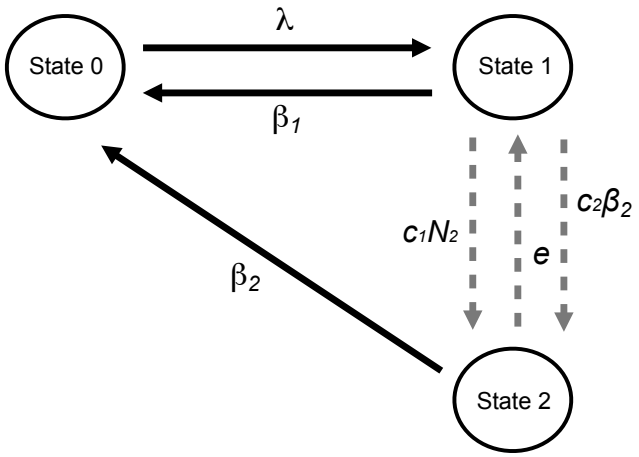

FIGURE 1. Transitions between patch states for a metapopulation living in a dynamic landscape. States 0, 1 and 2 correspond to patches being unsuitable and unoccupied, suitable and unoccupied, suitable and occupied, respectively. Patch dynamics (solid black arrows) are governed by restoration rates of patches, λ and destruction rates of patches, β_1 and β_2. Metapopulation dynamics (dashed gray arrows) are governed by colonization and extinction rates $c_1 + c_2\beta_2$ and e.

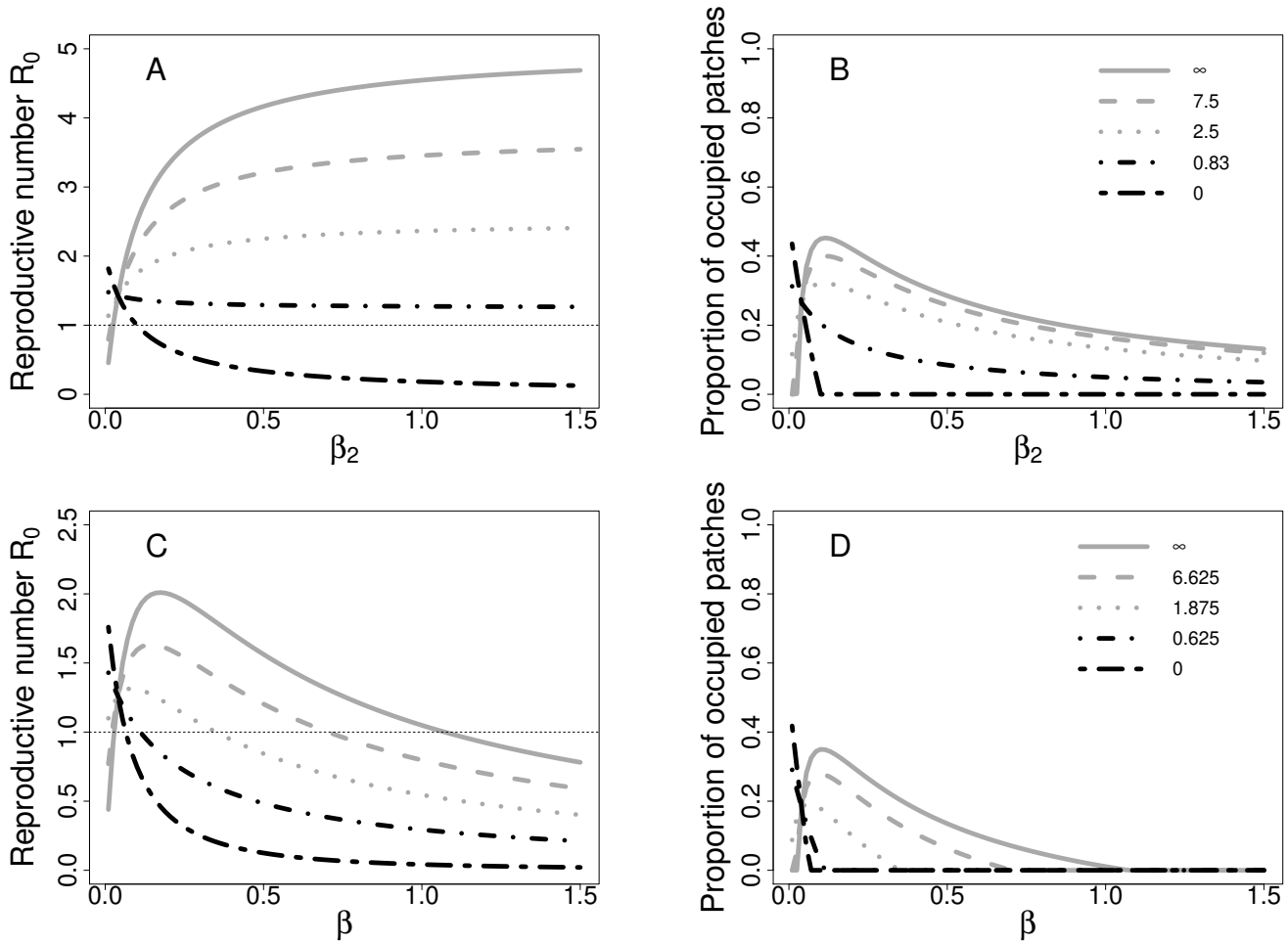

FIGURE 2. Metapopulation persistence and patch occupancy when only patch occupancy causes shifts in patch suitability (A, B) and when shifts in habitat quality are independent of occupancy (C, D). In (A) and (B), reproductive number for an individual patch during its lifetime and equilibrium patch occupancy are plotted as functions of the rate β_2 at which occupied patches become unsuitable. Gray lines represent cases where $c_2 > c_1/e$ and black lines cases where pulsed dispersal produces less colonizers ($c_2 < c_1/e$). In (C) and (D), reproductive number for an individual patch during its lifetime and patch occupancy are plotted as functions of the rate at which suitable patches become unsuitable ($\beta_1 = \beta_2 = \beta$). Gray lines represent cases where $c_2 > c_1/e + c_1/\lambda$ and black lines where $c_2 < c_1/e + c_1/\lambda$. The gray tiny dotted line in (A) and (C) is the thresholds for metapopulation persistence. Parameter values: $\lambda = 0.3$; $e = 0.1$; $c_1 = 0, 0.5, 1, 1.5$ and $c_2 = 5, 3.75, 2.5, 1.25, 0$ respectively.

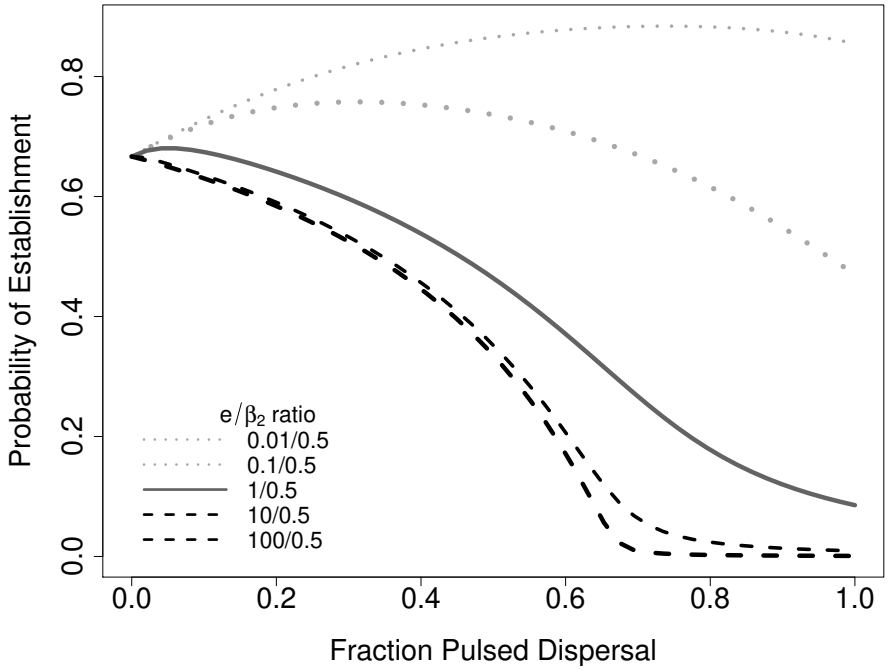

FIGURE 3. Establishment probability as a function of the fraction of colonization due to pulsed dispersal. Different lines correspond to different ratios of habitat lifetime to population lifetime (e/β_2): in light gray dotted lines habitat lifetime is faster than population lifespan and in black dashed lines population lifespan is shorter than habitat lifetime. Parameter values: $e = 0.01, 0.1, 1, 10, 100$; $\beta_2 = 0.5$; $\lambda = 0.3$; $R_0 = 3$; $c_2 = \alpha(c_1/\beta_2)$, where α is the fraction of colonization events due to pulsed dispersal.

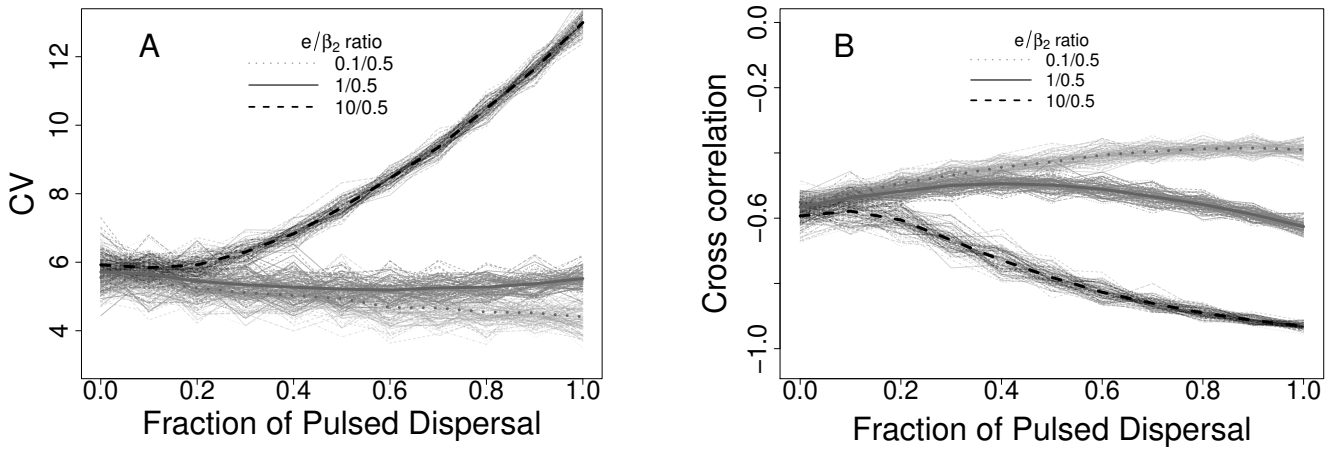

FIGURE 4. Covariance structure of in patch occupancy for the stochastic model. (A) Estimated variance in patch occupancy and (B) temporal synchrony between unoccupied and occupied patches (cross correlation coefficients) as a function of the fraction of colonization due to pulsed dispersal. Gray dotted, dark gray solid and black dashed dark lines represent respectively habitat lifetime faster than population lifespan, same rates of habitat lifetime and population lifespan and population lifespan shorter than habitat lifetime. Light line colors correspond results for 100 simulations in 1000 time units. Parameter values: $N = 1600$; $e = \{0.1, 1, 10\}$; $\beta_1 = \beta_2 = 0.5$; $\lambda = 0.3$; $R_0 = 3$; $c_1 = R_0(e + \beta_2)/\ p_1^*$; $c_2 = c1/\beta_2$.

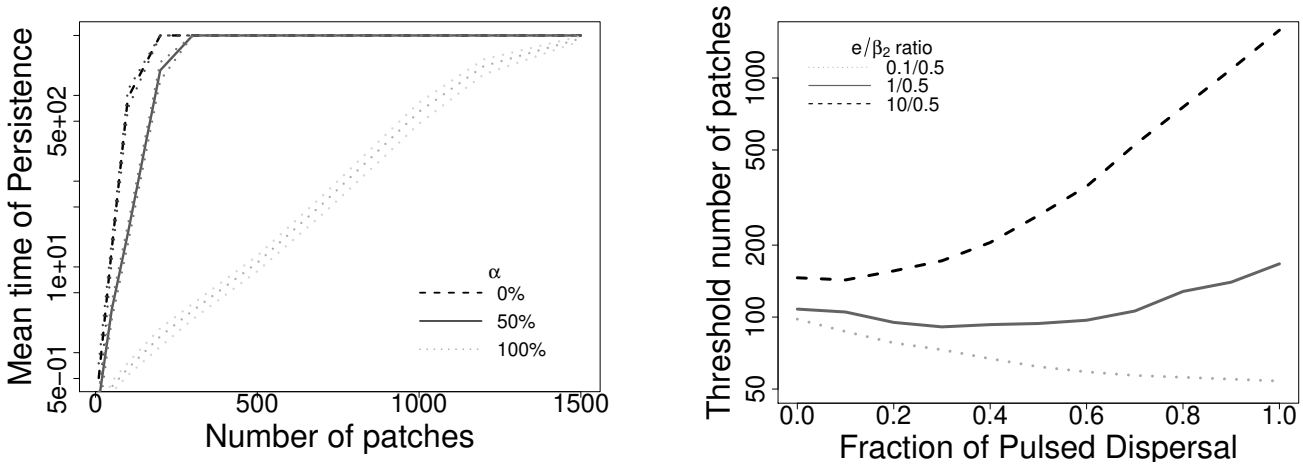

FIGURE 5. Influences of dispersal mode, habitat lifetime and population lifespan on metapopulation viability and critical landscape size.(A) Mean (95% CI) of persistence time of populations in which lifespan is shorter than habitat turnover rates ($e/\beta_2 = 10/0.5$) in function of different landscape size for 0%, 50% and 100% fractions of pulsed dispersal. (B) Mean of habitat availability threshold for landscapes giving metapopulation persistence in 90% of replicates as a function of the fraction of colonization occurring through pulsed dispersal. In (B) different curves represent variations in critical size of a dynamical landscape for different levels of e/β_2 ratios: light gray dotted line represents habitat lifetime faster than population lifespan; dark gray solid line represents the same habitat lifetime and population lifespan, and the black dashed line represents population lifespan shorter than habitat lifetime. Lines in (A) and (B) represent the result of means (*log* transformed) of 100 simulations during 5000 time units. Parameter values: $e = 10$; $R_0 = 3$; $\beta_1 = \beta_2 = 0.5$; $\lambda = 0.3$; $c_1 = R_0(e + \beta_2)/\ p_1^*$ and $c_2 = \alpha(c1/\beta_2)$, where α is the fraction of colonization events due to pulsed dispersal

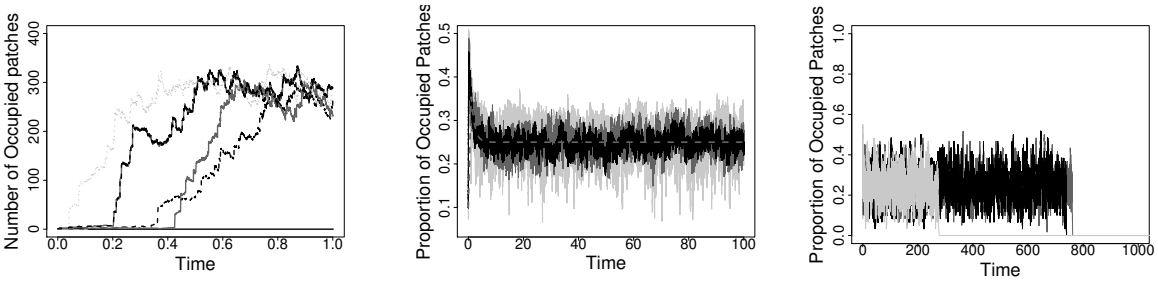

Fig.A.1: Simulations results for (A) establishment, (B) stochastic fluctuations (SDE) against the mean field equation (ODE), and (C) extinction events. In (A) different lines correspond to results of multiple simulations showing failed invasion attempts as well as successful ones. In (B) and (C) black, dark gray and gray lines correspond to 0%, 50% and 100% fraction of pulsed dispersal after patch disturbance. The gray dotted line in (B) corresponds to mean field patch occupancy dynamics. Parameter values, in (A) $N = 1000$; $\alpha = 0.5$; e=10 in (B) $N = 1000$; e=10 and in (C) $N = 60$; e=1 and in all panels $\beta_1 = \beta_2 = 0.5$; $\lambda = 0.3$; $R_0 = 3$;$c_1 = R_0(e + \beta_2)/\ p_1^*$; and $c_2 = c1/\beta_2$.

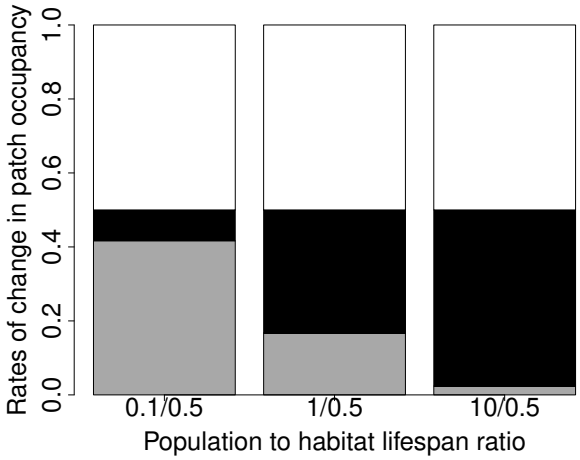

Fig.A.2: Frequency of extinction events (black), shifts in habitat quality (gray), and colonization events (white) for the stochastic model. Because the simulations started at patch occupancy equilibrium, the means of simulations for all fraction of pulsed dispersal are similar and corresponds to equilibrium given by deterministic model. Parameter values, $N = 1600$; $e = \{0.1, 1, 10\}$; $\beta_1 = \beta_2 = 0.5$; $\lambda = 0.3$; $R_0 = 3$; $c_1 = R_0(e + \beta_2)/\ p_1^*$; $c_2 = c1/\beta_2$.